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OBSERVATIONS ON THE DEVELOPMENT AND GERMINATION OF THE SEED IN CERTAIN POLYGONACEAE

EDWARD F. WOODCOCK

The Polygonaceae have been included by Harz (7, p. 1072) under the "Curvembryonaten" which he speaks of as being furnished with an abundant perisperm, and laterally placed embryo. The term "perisperm" is applied to the remaining portion of the nucellus in a mature seed. Harz (p. 1102) carefully figures and describes the buckwheat seed, considering the entire storage region as perisperm, and stating that the same relation holds in species of *Rumex*.

Johnson (11, p. 334), evidently influenced by the work of Harz, was led to believe that there is a rather close relationship between the Polygonaceae and the Piperaceae, in which family he observed perisperm. In these Piperaceae he looks upon the very abundant perisperm as the real storage region, it being separated from the embryo by a layer of endosperm, which, instead of acting as a storage region, serves to digest and pass on food material to the embryo from the perisperm. In an earlier paper (10, p. 368) Johnson had already pointed out this restriction of the endosperm in *Saururus* and suggests the probability of a similar relation existing in all seeds furnished with a large amount of perisperm as in Polygonaceae, Chenopodiaceae, Phytolaccaceae, Caryophyllaceae, etc.

Kraemer (12, p. 262) in his text-book merely mentions the fact that the Polygonaceae possess a "mealy" endosperm, without going into a discussion of the seed development. He also figures in detail a transverse section of *Fagopyrum esculentum*, but states nothing further in regard to its morphology.

Two years later Stevens (18, pp. 59–65) made a detailed study of the morphology of the seed of buckwheat to determine whether, as suggested earlier by Harz and Johnson, perisperm did really exist in the mature seed. After careful investigation he was convinced that no perisperm existed in this seed at maturity. The fact that Humphrey (9), working on the Scitaminales, found, in closely related genera, various amounts of endosperm, suggested to Stevens that even though there is an absence of perisperm in *Fagopyrum esculentum*, the other members of the Polygonaceae may perhaps be characterized by perisperm at maturity. In the order Scitaminales Humphrey found that the Musaceae are characterized by an abundant starch-bearing endosperm, the Zingiberaceae and Cannaceae by a thin layer of aleurone or proteid-containing endosperm, and the Marantaceae by an apparent absence of endosperm in the mature seed. Humphrey also pointed out a variation even in a single family. Among the Musaceae, *Heliconia* shows a narrow layer of functional perisperm around the endosperm; while in *Strelitzia*, the perisperm becomes reduced to a thin layer of broken down tissue.

Among the earlier writers who have dealt with the Polygonaceae, Strasburger (20), in 1879, described in detail the development of the mature embryo sac in *Polygonum divaricatum*, taking up the arrangement of the cells in the flower rudiments, the plan of the ovule and embryo sac and the development of the latter. He includes a brief description of the formation of the integuments and the course of the vascular bundle in the ovary and ovule, but says nothing regarding the morphology of the seed in its later development. In a later work (1902), Strasburger also simply describes *Polygonum orientale* with respect to the arrangement of the parts at the time of the mature embryo sac.

Dammer, writing on the Polygonaceae in Engler and Prantl (6), described the fruit and seed of Polygonaceae, dealing with the adaptations for dissemination, rather than the morphology of the seed.

The writer has made a careful study of certain genera of the Polygonaceae to determine if the absence of perisperm as a storage tissue noted in *Fagopyrum* by Stevens (1912), holds in the mature seed of other Polygonaceae. The genera under observation have been *Polygonum*, *Polygonella*, *Rumex*, and *Rheum*. In each of these genera, one or more representative species have been taken into consideration.

The material on which this study was made was collected during the summer of 1911 and 1912, and killed in weak chromo-acetic acid. Sections were cut about 12 μ in thickness and stained with Delafield's haematoxylon. An interpretation of the exact position and shape of the embryo in the mature seed was gained by free hand dissections under the binocular microscope.

A further study of the changes which occur in the seed tissues of *Fagopyrum*, *Polygonella*, *Polygonum*, and *Rumex* during the process of germination has also been carried on by the writer.

It was at the suggestion of Prof. A. W. Evans that this work was carried on, and it is to him that the writer is indebted for valuable assistance in all parts of the work, and to Dr. G. E. Nichols for liberal aid in the preparation of material.

Description and Discussion of the Morphology of the Seed

The growth and differentiation which take place in the ovules in response to the stimulus of sexual union have been studied in detail in the seeds of representative species in each of the genera *Polygonum*, *Rumex*, *Polygonella*, and *Rheum*, special emphasis being laid upon the morphology of the structures present in the mature seed.

Polygonum

P. Persicaria, *P. aviculare*, *P. tenue*, *P. sagittatum*, and *P. Convolvulus* were studied in detail, but as there was a marked similarity in their development it will be sufficient to describe in detail only one species, *e. g.*, *P. Persicaria*. The points of difference between this type and the remaining species mentioned will be taken into consideration.

The early development of the embryo in *P. Persicaria* up to the stage at which the cotyledons begin to be differentiated appears to correspond almost cell for cell with the typical *Capsella* embryo. The suspensor of *P. Persicaria*, however, consists of only two or three cells, whereas in *Capsella* it is made up of seven or eight cells.

Very soon after fertilization, free nuclear division begins in the embryo sac, and when the embryo has reached the octant stage, shown in *figure* 1, the cytoplasm of the endosperm containing about 30 free nuclei forms a granular layer, *EN*, lining the embryo sac, *K*. A single outermost layer of the nucellus, *N*, extending to the micropyle, differs markedly from the rest. At some period before fertilization occurs, this layer becomes differentiated and is made up of closely packed, prismatic cells, characterized by rather dense granular contents and an absence of vacuoles. The embryo sac, occupying a central position in the nucellar tissue extends nearly to the base. The micropylar portion of the sac is expanded being separated from the inner integument only by the differentiated nucellar layer.

As development proceeds growth and nuclear division occur most rapidly in the micropylar portion of the endosperm, in the region about the developing embryo. At about the time of the first indication of cotyledons in the embryo, cellular formation appears in this region, giving rise to a thin layer of cells around the embryo and also extending across the embryo sac below it. As further cell formation proceeds in the endosperm, a marked differentiation becomes apparent. At the stage shown in *figure* 2, the cell formation has proceeded until a portion of the endosperm, *EN*, about 6 cells thick extends across below the embryo. The endosperm above and at the sides of the embryo consists of a layer one or two cells thick, while below the thickest region, the endosperm again becomes gradually thinner and thinner, until at the base, for about one-fourth its length it no longer shows cell division but consists of a layer of nucleated cytoplasm, enclosing the large central sap cavity. This cytoplasmic layer merges into a cylindrical haustorium-like mass of dense protoplasm, *H*, at the base of the embryo sac, which apparently has no special function, as it undergoes very little change in the later development of the seed.

This marked differentiation of the endosperm into a cellular and non-cellular region, presented a condition similar to that described by Hofmeister (8, p. 185) and Strasburger (19, p. 101) in which the first division of the primary endosperm nucleus gives rise to a two chambered embryo sac, in only one of which the endosperm is developed.

A secondary differentiation in the cellular portion of the endosperm becomes evident very soon after the stage just described; the outermost layer assuming the appearance and function of a "cambium" layer which cuts off cells only from the inner side (*fig.* 2*a*, *CA*). Chamberlain (4, p. 344), in the developing endosperm of *Dioon edule*, and Stevens (18, p. 61), in *Fagopyrum esculentum*, have found similar conditions. These "cambium" cells divide rapidly, forcing the newly formed cells toward the center and downward as shown in *figure* 2*a*. The size of the sap cavity is thus diminished through the active growth of these cells. Very soon after the stage shown in *figure* 2, the cotyledons appear in the embryo, the sap cavity continuing to become smaller, until it becomes completely obliterated. As the embryo continues in development at the expense of the endosperm, it comes to lie in one angle of the seed with the faces of the cotyledons parallel with the flat surfaces of the seed as shown in *figure* 3. At this stage the endosperm cells differ considerably in appearance. The "cambium" cells and those adjacent are prismatic and densely filled with protoplasm, no intercellular spaces being present. Nearer the center the cells are larger, vacuolated, polyhedral and often binucleate, intercellular spaces also appearing. Numerous starch grains appear in the cells of this central tissue. Of the cells about the embryo only the distorted remains appear. Stevens (18, p. 63, fig. 4) has represented a similar condition for *Fagopyrum esculentum.*

The differentiated outermost layer of the nucellus has persisted in an actively growing condition up to this stage keeping pace with the growth of the ovule. The cells of this layer have not divided, but the individual cells, except at the micropylar region, have become tangentially enlarged and vacuolated. As the embryo approaches maturity, these cells become more and more coarsely vacuolate, until in the mature seed only the crushed remains of this layer are evident. Stevens, p. 63, has figured a similar condition for *Fagopyrum esculentum.* The micropylar portion of this layer is made up of a single plate of much thicker cells undergoing no very appreciable change after the time of fertilization. Practically all of the remaining nucellar tissue has been destroyed, only a comparatively few crushed and distorted cells remaining around the haustorium-like structure earlier mentioned (*fig.* 3, *N*).

The persistence of the differentiated outer layer in an actively growing condition during the entire endosperm development, and the fact that it is characterized by dense granular contents, suggests that it serves a nutritive function. Coulter and Chamberlain (5, p. 178) have termed this layer the "nutritive jacket." The inner integument usually gives rise to this layer; however, Billings (2, p. 278), as one exception, describes, in *Armeria plantaginea*, such a layer, which he terms "tapetum," as derived from the outer portion of the nucellus. Stevens (p. 62) has described in *Fagopyrum esculentum* a similar condition. Billings finds in *Erodium gruinosum* a "tapetum" made up of two layers, the inner one arising from the nucellus, and the outer from the integument.

Lloyd (13, p. 103) has shown that in the date, nutritive material is distributed to the developing endosperm through the integuments to some extent. In *P. Persicaria*, however, the integuments apparently undergo very little differentiation, remaining as rather thin uniform structures, each consisting of but two layers of cells. As the ovule of *P. Persicaria* is furnished with no vessels for the transfer of nutritive material from the chalaza to the growing endosperm, it is quite conceivable that the differentiated outer layer of the nucellus assumes this function. Further, the more rapid endosperm development in the micropylar region is evidently due to the fact that food material is brought there by way of this layer, since the broken-down cells of the undifferentiated nucellar tissue form a barrier to any passage of food substance through that channel.

As the seed approaches maturity, a further differentiation occurs in the endosperm. After the "cambium" layer ceases cutting off starch-storing cells, it divides further by anticlinal walls; thus giving rise to a layer of short, thin-walled prismatic cells, which, in the micropylar region, undergo further division, developing to the exclusion of the starch-storing endosperm and passing abruptly into the latter. At the maturity of the seed, shown in *figure* 4, the cells of this layer, *A*, are densely filled with granular contents, but contain no starch. This is an aleurone layer, the "eiweisshaltige Zellen" of Harz. Except for this aleurone layer the remaining portion of the endosperm, *EN*, consists of large, thick walled cells, closely packed and filled with starch grains, which by their pressure cause the nuclei to become flattened and irregular in outline.

In the mature seed, which is 2 mm. wide and 2.5 mm. long, the cotyledons of the embryo are flattened and slightly broader than the hypocotyl. The entire embryo occupies a cavity at one side of the seed (*figs.* 4, *E*, and 9, *C*), this cavity having been formed by the continuous growth of the embryo at the expense of the endosperm. The cells lining this cavity are somewhat broken down and irregular in outline due to their depletion by the developing embryo.

The only vestige of the original nucellus present in the mature seed as perisperm is a mass of broken-down tissue at the base of the seed (*fig.* 4, *N′*) and the crushed remains of the nutritive layer. It is interesting to note that during the later development of the seed these tissues have apparently served no function, and do not represent a storage region, this function being entirely carried out by the endosperm with its aleurone layer.

The thin, uniform integuments, in the development of the seed to maturity, have become closely compressed, so that only their crushed remains appear in the mature seed (*fig.* 4, *I*).

The seed, at maturity is enclosed in a thick hard coat, consisting of the cutinized epidermal layer and the compressed inner layers of the ovary (*fig.* 4, *O*).

If attention is now turned to a consideration of *Polygonum aviculare* and *Polygonum tenue*, it is seen that the development of these two species appears practically identical, therefore, the variations from the type will be followed only in *Polygonum aviculare.* The early stages are essentially the same, *figure* 1 representing very well the condition at the octant stage for both species. The nucellus of *P. aviculare*, however, becomes degenerated to a slightly greater extent. As growth proceeds beyond this point, the method of development is the same but the rapidity of endosperm formation is much greater. At the time of the first indications of cotyledons in the embryo, the embryo sac is already filled with cellular endosperm, and the nucellus has been reduced to a few crushed cells at the base of the seed, and the nutritive layer. The haustorium-like mass of protoplasm at the base of the seed is much broader. The suspensor of the embryo is made up of four cells, instead of only two as in the majority of seeds of *P. Persicaria.*

The later development follows much the same plan, the growing embryo coming to lie in one of the corners of the seed. At maturity (*figs.* 5 and 8), the seed is 2.35 mm. long and 1.26 mm. wide. The embryo is longer than in *P. Persicaria*, and extends across the chalazal region. The cotyledons are semicircular in outline (*fig.* 8, *C*) and the cotyledon away from the starchy endosperm lies with its back against the chalazal region of the seed. As growth has proceeded, the cotyledon next the endosperm has grown down over the other cotyledon. The cylindrical, massive hypocotyl is the same width as the cotyledons at the base of which appears a well-developed, cylindrical plumule (*fig.* 5, *P*).

Polygonum Convolvulus and *Polygonum sagittatum* agree in most respects with the type. At the octant stage of *P. Convolvulus* (*fig.* 6), however, the ovule is much broader and the integuments relatively thicker than in *P. Persicaria.* At maturity, the cotyledons are rather broad and flattened, the edges pressing against the base of the seed with the tips well past the middle line of the seed. The position of the cotyledons with respect to the chalazal region of the seed agrees with the condition found in *P. Persicaria*, but differs from that found in *P. aviculare* and *P. tenue*, in which the back of the outer cotyledon lies pressed against the chalazal region of the seed. *Figures* 7 and 10 represent the mature condition found in *P. Convolvulus*, and may also serve the same purpose for *P. sagittatum*, except that in the latter species the cotyledons are somewhat broader.

Rumex

In this genus, the two species studied, *Rumex crispus* and *Rumex Acetosella*, are essentially alike in their development, and follow to maturity the same plan as that described for *Polygonum Persicaria.* Some interesting differences from the type appear in the mature seeds.

The embryo of *R. crispus*, in its development to maturity, comes to lie usually at one side of the seed (*figs.* 11, *E*, and 13, *C*) with the back of the outer cotyledon pressed against a flat surface of the seed and the chalazal region. The massive, somewhat flattened hyocotyl is the same width as the cotyledons which are semicircular in section. The mature seed is 2.45 mm. long and 1.55 mm. wide.

In *Rumex Acetosella* the mature embryo (*fig.* 12, *E*) usually occupies the same relative position at one side of the seed as in *R. crispus.* The embryo is very much more curved, corresponding with the shorter and relatively broader seed, which is 1.2 mm. long and .9 mm. wide. The cotyledons, similar in section to those of *R. crispus* (*fig.* 13, *C*), extend across the chalazal region almost to the angle opposite.

The position of the embryo against a flat surface of the seed is apparently not a fixed character in *Rumex*, for the writer in examining a number of seeds of both the above species, found, in several cases, the embryo situated in an angle of the seed. This is a marked contrast to the conditions found in the genus *Polygonum*, for there the position of the embryo seems to be a fairly fixed character.

Polygonella

The single species studied, *Polygonella articulata*, showed some very marked differences from the selected type, *Polygonum Persicaria*, although some stages in the development correspond very closely.

The early development up to the octant stage agrees with the type, except in the length and structure of the suspensor. At this stage, shown in *figure* 14, the suspensor, *T*, is about two thirds the length of the embryo sac, and is made up of large inflated cells. The lower two thirds consists of two rows of cells, while the upper micropylar portion is made up of a single chain of four or five cells.

As development proceeds growth and nuclear division in the endosperm is uniform in the micropylar region, and about the periphery of the embryo sac. At about the time that the meristematic regions become differentiated in the embryo, cell formation appears in the free endosperm, giving rise to the uniform layer of cellular endosperm. At the stage shown in *figure* 15, in which the cotyledons are becoming differentiated, this endosperm layer, *EN*, has become two cells thick, the outermost layer being differentiated into a "cambium" as in *Polygonum Persicaria.* The suspensor has become somewhat shriveled and the embryo imbedded in the layer of cellular endosperm lining the embryo sac.

The growth of the endosperm from the stage just described proceeds as in *Polygonum Persicaria.* At the stage shown in *figure* 16, the embryo is situated well down toward the base of the seed. The space about the embryo is continuous with a long narrow cavity, *CY*, extending to the micropyle. This cavity contains the shriveled remains of the suspensor and serves as a path for the later elongation of the hypocotyl. *Figure* 17 shows a later stage in which the hypocotyl and fleshy cotyledons have become quite well differentiated, and the cavity containing the shriveled suspensor has become somewhat larger.

The further growth and differentiation of the various tissues of the ovule proceed as in the type. The mature seed (*figs.* 18 and 19) which is 1.8 mm. long and .8 mm. wide, presents some differences in the tissues formed. At the micropylar portion of the aleurone layer (*fig.* 18*a*, *A*) appears an outer region consisting of prismatic cells containing dense granular contents, and an inner region consisting of irregular cells filled with a watery solution. The depleted condition of these cells has evidently been brought about through absorption by the surrounding tissues. The embryo, in its mature condition, is usually situated in an angle of the seed (*fig.* 19, *C*). The position of the embryo in this species seems to be quite as unstable a character as in *Rumex*, for, in a number of cases examined, the mature embryo occupied a position against one of the flat surfaces of the seed.

The relatively long hypocotyl passes into the broader, fleshy cotyledons, which are elliptical in cross section and lie pressed against the base of the seed, with their faces at an angle of about 45 degrees to a plane cutting the long axis of the seed at right angles (*fig.* 18, *C*).

This position of the cotyledons is in marked contrast to the condition found in *Polygonum* and *Rumex.* In *P. Persicaria*, *P. Convolvulus*, and *P. sagittatum*, the edges of the cotyledons are pressed against an angle of the seed and the chalazal region, while in *P. aviculare*, *P. tenue*, *Rumex crispus*, and *R. Acetosella*, the back of the outer cotyledon presses against a face of the seed and the chalazal region.

Rheum

A single species, *R. Rhaponticum*, was taken into consideration. Its development to maturity corresponds in many respects to that of *Polygonum Persicaria*, but some differences are evident, which deserve special attention.

The mature fruit is broadly three winged, a feature quite characteristic for this genus. The length of the fruit is 5 mm. and the width, exclusive of the wings, 3.6 mm. The inner wall of the ovary so indents the testa of the seed as to cause it to be very much longitudinally folded, as shown in *figure* 21.

The aleurone layer (*fig.* 20, *A*) instead of being several cells thick, as in the type, consists of a single layer of cells. The mature embryo, occupying a central position (*figs.* 20 and 21) is relatively larger than the type, corresponding with the larger size of the seed. Stevens found the mature embryo of *Fagopyrum esculentum* also occupying a medium position in seed. *Rheum* and *Fagopyrum* are the only Polygonaceae according to the investigations up to the present time, possessing this character. The mature seed of *R. Rhaponticum* is abruptly narrowed at the apex, so that the short, massive, cylindrical hypocotyl practically fills the micropylar region of the seed, only the aleurone layer separating it from the testa (*fig.* 20). In *R. palmatum*, Lubbock (14, p. 436) found a similar condition, but in *R. officinale*, he found the seed not abruptly narrowed at the apex. The broad, thin cotyledons (*fig.* 21, *C*), which are about two and one half times the length of the hypocotyl, do not extend to the base of the seed, as shown in *figure* 20. They are sometimes more or less folded longitudinally. Lubbock describes an exceptional condition in *R. palmatum* in which the cotyledons are oblique to one another, and in one instance they were twisted at right angles to one another so as to occupy the three angles of the seed and thus attain the greatest possible size.

A very interesting feature in *R. Rhaponticum* is the petioled condition of the cotyledons at the base of which is a quite well developed plumule. In *Polygonum*, *Polygonella*, and *Rumex*, the cotyledons spring directly from the hypocotyl without developing distinct petioles.

GERMINATION OF CERTAIN POLYGONACEAE

These investigations were carried on in order to gain a knowledge of the fate of the embryo, starchy endosperm, and aleurone layer in the mature seed during germination. Most of the seeds were germinated between wet filter papers, a few, however, were placed in the soil. The latter were used in determining the relation of the very young seedling to the surface of the soil. The material, on which the study of the changes occurring in the germinating seeds was carried on, was cut in sections 18–22 μ in thickness and stained with Delafield's haematoxylon and orange G.

Rumex crispus

The seed shows no external change during the first two days, but significant internal changes are occurring. The cells of the thickened micropylar region of the aleurone layer first show very great activity. In the ungerminated seed the entire layer is made up of short prismatic cells, containing large nuclei and filled with deeply staining cytoplasm. The cells of the micropylar portion now become much enlarged and numerous fine granules appear scattered quite uniformly through the fine alveolar cytoplasm. In certain seeds the granules were surrounded by a clear liquid. This increase in size of the cells is brought about not only by osmotic pressure but also by an actual increase of cell wall structure.

It is quite probable that the occurrence of these granules in the cytoplasm of the aleurone layer is associated with the secretion of a digestive ferment as is true in the digestive cells of certain other seeds and in the digestive glands of animals. Brown and Morris (3), through observation on the changes in the scutellar epithelium of the barley grain, find that their thin-walled, columnar cells in the process of germination undergo a significant change. Before germination begins, the cell contents are finely granular and the large, elliptical nucleus lies near the base of the cell with its longer dimensions across the cell. Within a few hours after germination begins the very fine granules in the protoplasm become much larger and coarser and increase in number to such an extent that the formerly conspicuous nucleus is almost obscured. This granularity is maintained until the endosperm is almost exhausted of its reserve materials, then the protoplasm becomes clear and transparent, the nucleus having disappeared.

Torrey (22), working on the cytological changes accompanying the secretion of diastase in the epidermal cells of the scutellum in maize, finds granules appearing in the cytoplasm during germination very similar to the condition found by Brown and Morris in the diastase secreting cells in the barley. In both these cases the nucleus finally disappears when the cell has exhausted itself after long continued secretion. In *Rumex* the writer was unable to follow the earlier changes undergone by the nucleus; however, it was noted that the nuclei lose their staining power and finally disappear as the secreting cells become exhausted. It is, nevertheless, quite probable that the nuclei do play an important role in the production of the ferment. Torrey gives a very interesting interpretation of the origin of these granules in the epithelial cells of the scutellum in maize. At the beginning of germination the nuclei of these cells contain dark staining granules, which are ejected into the cytoplasm through minute breaks in the nuclear membrane. These granules at first spread through the cell, but later collect at the end of the cell next to the endosperm, where they are ultimately dissolved. In *Rumex* the granules are distributed quite uniformly through the cytoplasm of the secreting cells and no such origin as Torrey describes is evident. He also notes an enlarged condition of the secreting cells similar to that which occurs in *Rumex*. He evidently considers this enlargement to be due merely to osmotic pressure without an increase of cell wall structure as the writer believes to be the case in *Rumex*. He suggests (p. 430) that the osmotic activity is very likely set up by some substance secreted in the cell at this time. The protein nature of diastase prevents it from being as osmotically active as other less complex substances, as for instance organic salts or acids, which when present in the cell exercise a strong osmotic attraction. Nevertheless, the enlargement of the cell occurs when the nucleus has become completely filled with these granules. The formation of some organic acid during the great metabolic activity of the cell may be a possible explanation of this phenomenon. This hypothesis is further supported by the fact that diastase, to be especially effective as a ferment in physiological experiments, must be dissolved in a slightly acid liquid.

In contrast to the condition found in the plant kingdom, Mathews

(15) has found in the animal kingdom that the nucleus of the pancreatic cell does not play an active role, but indirectly controls the zymogenesis. Haidenhain and Korshelt consider that the changes in position and size of the nuclei during secretion are signs of functional nuclear metabolism.

There is associated with the increase in size and granularity of the aleurone cells in *Rumex* a gradual change in the endosperm and embryo. This change is seen in the endosperm as a slight depletion of the starch cells next to the thickened micropylar portion of the aleurone layer and next to the embryo. Perhaps the depletion in the latter region is entirely due to a ferment secreted by the embryo itself. Newcombe (16, p. 71) has found in the buckwheat that the cotyledons do actually secrete a ferment which has a weak solvent power on wheat-starch grains, and on the membranes of the barley endosperm. This may be true for *Rumex* but it seems more probable that the aleurone cells, which at this time have every appearance of active digestive cells, are secreting an enzyme which is the principal agent in the dissolution of the starch in the endosperm. This enzyme diffuses to the starchy endosperm in the watery solution about the embryo. As a result of the action of the enzyme on the starch, there is a conversion of the insoluble starch into a soluble form, in which form it is absorbed by the embryo. In connection with the transfer of the dissolved starch to the germinating embryo an interesting phenomenon may be noted. As the carbohydrate solution is absorbed by the growing embryo, instead of being entirely consumed at once by the growing embryo, as is assumed to be the case in endosperm-containing seeds, a part of this absorbed solution is converted back into the insoluble form and stored in the cells of the embryo in the form of compound starch grains. The depletion of the starch cells continues, consecutively towards the outside of the seed, the depleted endosperm cells in contact with the embryo becoming collapsed by the pressure of the latter. As the micropylar portion of the aleurone layer becomes exhausted through continued secretion, the basal thinner portion comes into activity, each individual cell acting independently of those adjacent.

If attention is now turned to a consideration of the changes in the embryo associated with the activity of the aleurone layer and the dissolution of the starch, it is seen that important changes are taking place. There occurs a rapid elongation of the embryo. This elongation forces the coat of the fruit apart at the apex, the break appearing at the angles of the fruit. As the embryo increases in size, the tip and then the whole radicle appears outside the fruit, as shown in *figure 22*. In so doing the micropylar portion of the shriveled testa, *D′*, is either pushed aside or carried outside a short distance with the radicle, *R*. As the radicle increases in length, the increase in size of the aleurone cells mentioned above, causes the micropylar portion of the layer, *L*, to appear outside the fruit and clasp the radicle, thus preventing any of the dissolved food material escaping from the seed in its passage from the endosperm to the embryo. This collar-like structure must also prevent to a great extent the entrance of water from without, which would dilute this food material, or bacteria and fungi which would cause its destruction.

As the radicle of the seedling continues to elongate it grows downward (*fig.* 23, *R*) and enters the soil, there becoming anchored by numerous root hairs and secondary roots. There occur at the same time, an elongation and broadening of the cotyledons, and a slight differentiation of the stalks. As germination continues the basal portion of the cotyledons emerges from the seed (*fig.* 24). By this time, the plumule which was hardly differentiated in the mature embryo, has attained a length of about 2 mm. and is cylindrical in form (*fig.* 24, *P*). The vascular system of the young seedling, which was undifferentiated in the mature embryo, has now become quite clearly differentiated. As the elongation of the cotyledons is occurring, the hypocotyl increases in length, raising the cotyledons with the seed adhering to the surface of the soil. At the stage shown in *figure* 24 the starch has all been absorbed from the starchy endosperm except within the regions included by the dotted line. The depleted cells retain practically their normal shape, only being broken down as the cotyledons increase in size and press against them. The inactive aleurone cells have lost their contents and their walls have become collapsed. Very soon after this the broadening cotyledons, which have now developed chlorophyll push off the wasted remains of the seed and become erect.

Fagopyrum esculentum

As the writer has not included a representative of the genus *Fagopyrum* in the morphological discussion of the Polygonaceae, a description of the mature fruit of the buckwheat, *F. esculentum*, will be given at this time.

The mature fruit is an achene, triangular in cross section and brownish black in color. The seed is large, filling the cavity of the ovary and conforming to its shape. The broad, thin cotyledons of the embryo are variously oriented from one angle of the seed to another, and present in cross section the appearance of a much distorted letter S. *Figures* 25 and 26 will give some conception of the complicated form of these cotyledons. The shortly petiolate cotyledons follow the interior of the testa for some distance outside the starchy endosperm, in close contact with the aleurone layer, which is uniformly one cell thick as in *Rheum Rhaponticum.* The cotyledons lie face to face with their midribs together and the width of the blade on one side of the midrib of each cotyledon is about twice that of the other side. As a result of this unsymmetrical form of the cotyledons, one of them extends beyond the other, the smaller half of each cotyledon being enclosed by the corresponding half of the other. In the mature fruit the radicle is rather large and tapers to an obtuse point, being completely enclosed by the basal portion of the cotyledons. The starchy endosperm is exceedingly irregular as a result of the peculiarly unsymmetrical nature of the embryo. The cotyledons do not extend quite to the base of the embryo sac in the mature seed according to Stevens, a space containing the remains of the undeveloped basal portion of the embryo sac, being always present in the chalazal region of the seed. In the mature seed the embryo has a well-differentiated vascular system, and the cotyledons have become differentiated into epidermal, palisade, and spongy tissue as well as conductive tissue.

The germination of *Fagopyrum esculentum* presents some very distinctive features although in some respects there is a marked similarity to the conditions found in *Rumex crispus.*

During the first two days there is very little external change except a slight enlarging of the seed. Internal changes are however very likely occurring for very soon the apex of the fruit becomes split along its angles. The aleurone layer shows marked activity in the enlarging of the cells especially in the micropylar and basal regions. As this enlargement occurs, the cytoplasm of the cells becomes alveolar and fine granules appear quite uniformly distributed through it much as in *Rumex crispus.* It is quite probable that there is associated with this activity of the aleurone layer, as suggested for a similar condition in *Rumex*, a secretion of a ferment which dissolves the starch of the endosperm. The digestion of the starch proceeds much as in *Rumex.*

The first evidence of the action of the ferment is seen in the depletion of the starch in the micropylar and basal regions. The dissolved starch is apparently not used up as fast as it is absorbed by the embryo but rather a part of it becomes converted back into an insoluble form in the cells of the embryo as already noticed for *Rumex crispus.* The depletion of the endosperm in *Fagopyrum* proceeds much as in *Rumex.*

As the starchy endosperm is being digested and absorbed by the embryo, the latter begins to increase in size. Very soon through the rent at the apex of the fruit the elongating hypocotyl and radicle appears outside the seed (*fig.* 25). The enlarged aleurone layer does not extend beyond the coat of the fruit as is the case in *Rumex.*

In sections of the seed at the stage in which the radicle is just appearing outside the seed, the elongated tannin sacs, mentioned by Solereder (17, p. 669) as occurring in species of *Fagopyrum* and *Polygonum*, are very evident. As further growth occurs these sacs increase markedly in length. Another interesting feature in the young radicle is the embryonic secondary roots which appear under the microscope as distinct slight elevations of the surface of the radicle.

As these changes are taking place in the hypocotyl and radicle, the cotyledons are increasing quite markedly in width and length, and to a slight extent in thickness. This increase in proportions is doubtless due to cell divisions as well as increase in cell size. The petioles or stalks of the cotyledons, which are so short in the ungerminated seed that they can be hardly distinguished as such, take on a slow growth as germination continues. In the stage shown in *figure* 25, they are only about .2 mm. in length. At about the fourth day of germination these stalks have become about 1 mm. in length and at their basal portion, merge into a swollen sheath-like structure of equal length (*fig.* 27, *SH*) which protects the developing plumule. As growth proceeds the basal portion of the cylindrical cavity of the sheath becomes lined in the region of the plumule with multicellular hair-like structures. The shape of the plumule (*fig.* 27, *P*) which is now about 4 mm. in length and almost fills the basal portion of the cavity, is that of an inverted top.

At the stage just discussed which is shown in *figure* 27, the basal portion of the cotyledons are loosely folded about the hypocotyl, which has now increased quite markedly in diameter. The increase in width of the cotyledons causes them to become much more folded than originally, and also causes the blades to extend nearly the whole distance around the inside of the seed as shown in *figure* 26. The starchy endosperm and the digestive aleurone layer have now become almost entirely depleted and the pressure of the enlarging cotyledons has collapsed the cells. Only the broken down remains of the aleurone layer are present inside the seed coat; and in the folds of the cotyledons at their basal portion, appear the distorted, empty starch cells (*fig.* 27, *EN*). The rapidly enlarging cotyledons soon push off the wasted remains of the seed and unfold, becoming oriented in a horizontal position. These cotyledons present now very much the appearance of regular foliage leaves; they are equipped with chlorophyll and all the tissues typical of foliage leaves.

Polygonella articulata

An attempt made in the early part of March to find some of the seeds in the sand about the dead plants resulted in the finding of only already germinated seeds. The hypocotyl and radicle had attained a length of about 12 mm. A number of the seedlings were allowed to develop further in the laboratory in order to make a study of the later stages in germination.

Upon examination of the earliest stages available conditions were found quite similar to those already described for *Rumex crispus*. At the stage shown by *figure* 28, the entire aleurone layer has become greatly enlarged. The cells in the thickened micropylar region show the characteristic granules of the digestive layer, while the remaining cells show a loose alveolar cytoplasm entirely free from granules. The enlarged condition of the aleurone cells causes the micropylar region of the layer to appear outside the seed coat (*fig.* 28, *L*) forming a collar-like structure as in *Rumex crispus*. This digestive layer behaves in a manner similar to that described in the preceding example. In the digestion of the starch there appears a marked difference, the starchy endosperm being depleted of its contents quite uniformly, instead of being progressive in its depletion. In contrast to *Fagopyrum* and *Rumex*, the digestive starch is all used up by the germinating embryo as it is absorbed, none of it is converted back into an insoluble form as in the above species. This digestion proceeds much slower than in the other species studied, consequently there is a corresponding slow growth of the young seedling.

As this growth proceeds the cotyledons gradually increase in length and become quite fleshy. The increase in size crushes the depleted starch cells and when the germination has reached the stage shown in *figure* 29, only the crushed remains of the endosperm and aleurone layer are present in the seeds. By this time the plumule, *P*, has increased in size, having attained a length of about 1 mm. and a width at its base of about .06 mm. It is conical in shape, the apex being slightly rounded. No multicellular hair-like structures are present about the plumule as in the preceding examples. Very soon after this the broadening cotyledons push off the seed remains, and become oriented in a nearly horizontal plane. The differentiation of the cotyledons into stalk and blade is only slightly evident at this time. Very little differentiation has occurred in the tissues of the cotyledons with the exception of the epidermis which has now become well developed.

Polygonum scandens

The ungerminated seed is very similar to that of *P. Convolvulus* already described in this paper. In following out the germination, conditions are found to be practically the same as described above for *Rumex crispus*, so a detailed discussion of the processes involved need not be entered into. A comparison of *figures* 23 and 24, representing certain stages in the germination of *Rumex crispus*, with *figures* 30 and 31, representing corresponding stages in *P. scandens*, shows how very similar in appearance are the methods of germination in the two species.

SYSTEMATIC RELATION OF THE POLYGONACEAE

Bentham and Hooker (1), include under the Curvembryeae, the Nyctaginaceae, Illecebraceae, Amaranthaceae, Chenopodiaceae, Phytolaccaceae, Batidae, and Polygonaceae. In these families the authors speak of the storage tissue outside the embryo as "albumen," without stating whether this tissue is endosperm or perisperm.

The writer sees no reason to doubt that Dammer, writing on the Polygonaceae in Engler and Prantl (6), has properly taken out the family from the Curvembryeae of Bentham and Hooker and placed it in a separate group termed Polygonales. Harz (7) agrees with Bentham and Hooker in placing the Polygonaceae in the Curvembryeae, and looks upon the storage tissue outside the embryo as perisperm rather than endosperm. This misinterpretation of the structure in the mature seed doubtless led him to place the Polygonaceae among the families characterized by perisperm containing seeds and curved embryos, comprising the Caryophyllaceae, Paronychiaceae, Portulaceae, Phytolaccaceae, Sclerenthaceae, Chenopodiaceae, Amaranthaceae, and Nyctaginaceae. In discussing the Curvembryeae, Harz states that he finds without exception in all the species studied an oily endosperm in slight amounts laid down about the axis of the embryo so that the radicle is surrounded by an endosperm sheath. The observations of the writer show that this structure noted by Harz is not so specialized a character as he implies, but rather represents the micropylar portion of the aleurone layer which is also continuous to the chalazal region of the seed.

Since the Polygonaceae are characterized by an abundant endosperm instead of perisperm as believed by early writers, there cannot be the close relationship between the Piperaceae and Polygonaceae that Johnson (11, 1902) suggests.

In his work on Seedlings, Lubbock (14) has followed the classification given by Bentham and Hooker and correctly interpreted the storage tissue in the seed of Polygonaceae as endosperm. Neither in the Polygonaceae nor in any of the other families which he included under the Curvembryeae does he refer to the aleurone layer of the endosperm or to the perisperm.

Among the Dicotyledons having a curved embryo and endosperm, the Nolanaceae, Solanaceae, Resedaceae and Convolvulaceae may be mentioned, but in each case there are other more prominent characters which cannot be overlooked and prevent them from being considered close relatives of the Polygonaceae.

The variations in the morphology of the Polygonaceae seed would seem to show that this family represents a more or less plastic evolutionary line. A primitive character is seen in case of the median embryo of *Rheum* and *Fagopyrum*, and a marked advance over this type in the curved embryo of *Polygonum*, *Polygonella* and *Rumex*. The orthotropous ovule prevailing in this family is also a primitive character. If some of the other characters of the Polygonaceae, as the wings developed on the fruit of *Rheum*, and the ochrea or tubular stipule occurring all through the family, are taken into consideration it is very evident that there has occurred some very high specialization.

SUMMARY

The outermost layer of the nucellus becomes transformed into a nutritive jacket at some period before fertilization. This layer apparently carries food material from the chalazal region to the developing endosperm. The remaining nucellar tissue becomes broken down comparatively early.

In *Polygonum*, *Rumex*, and *Rheum*, the cellular endosperm appears first in the micropylar region, while in *Polygonella* it appears uniformly about the periphery of the embryo sac. The cellular endosperm increases in extent by the activity of a cambium-like layer differentiated very soon after cell formation appears. Some time before maturity of the seed this "cambium" layer ceases cutting off cells and becomes differentiated into an aleurone-containing layer, which, in *Polygonum*, *Rumex*, and *Polygonella*, through further tangential cell division, becomes several cells thick in the micropylar region.

In *Polygonum*, *Rumex*, and *Rheum*, the suspensor is from two to four cells in length, while in *Polygonella* it is about twelve cells in length, the portion next to the embryo consisting of two rows of cells.

The embryo in its development to maturity comes to occupy a position either in the axis of the seed, an angle of the seed, or against one of the faces of the seed. The first position is seen in *Fagopyrum esculentum* and *Rheum Rhaponticum;* the second in *Polygonum Persicaria*, *P. Convolvulus*, *P. sagittatum*, *P. aviculare*, *P. tenue*, and *Polygonella articulata;* the third in *Rumex crispus* and *R. acetosella.* Only in *Polygonum*, *Fagopyrum*, and *Rheum* is the position of the embryo a fixed character.

The germination of *Rumex crispus*, *Fagopyrum esculentum*, *Polygonella articulata* and *Polygonum scandens*, shows that the aleurone layer has presumably a digestive function, secreting a ferment which converts the insoluble starch of the endosperm into a form available for the germinating embryo. The cells of the layer become much enlarged, and their cytoplasm finely alveolar and granular. In *Rumex*, *Polygonella*, and *Polygonum* this increase in size of the aleurone layer causes the micropylar portion to appear outside the seed coats.

In *Rumex* and *Fagopyrum*, the absorbed carbohydrate is temporarily converted back into starch in the tissues of the germinating embryo, the cotyledons being the principal storage region.

YALE UNIVERSITY

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EXPLANATION OF PLATES XLV–XLVIII

All *figures* drawn from median longitudinal sections, except *figures* 8, 9, 10, 13, 19, 21, and 26, which are from cross-sections. The following abbreviations are used: *A*, aleurone layer; *C*, cotyledons; *CA*, embryonic cells of endosperm; *CY*, cavity left by shriveled suspensor; *D*, depleted portion of aleurone layer; *D'*, remains of micropylar portion of integuments and nutritive layer; *E*, embryo; *EN*, endosperm; *F*, remains of suspensor; *H*, haustorium-like structure; *HY*, hypocotyl; *I*, integuments; *K*, embryo sac; *L*, enlarged aleurone layer; *N*, nucellus; *N'*, remains of undifferentiated nucellus; *NU*, "nutritive jacket"; *O*, mature seed coat; *OT*, mature seed coat plus remains of integuments; *P*, plumule; *R*, radicle; *SH*, sheath-like structure; *T*, suspensor.

FIG. 1. *Polygonum Persicaria*, showing the embryo in the octant stage and the endosperm in the free nuclear condition; × 53.

FIG. 2. *P. Persicaria.* The embryo showing the first differentiation of the cotyledons; the upper portion of the endosperm has become cellular, while no cell walls have appeared in the lower portion; haustorium-like structure evident at the base of the embryo sac; × 40.

FIG. 2*a*. Portion of longitudinal section of *P. Persicaria* seed at about the stage shown in *fig.* 2; only the outermost layer of the nucellus, the "nutritive jacket," remains functional; the endosperm shows an outermost layer of embryonic cells and a more central region of large vacuolate cells; × 248.

FIG. 3. *P. Persicaria.* A later stage in which the embryo sac has become completely filled with cellular endosperm, except at the base where the haustorium-like structure is seen; embryo at the side; × 31.

FIG. 4. *P. Persicaria.* Mature seed; endosperm filled with starch; aleurone layer present; nucellar tissue practically all obliterated; embryo at the side; dotted line indicates plane of cross section shown in *fig.* 9; × 31.

FIG. 5. *Polygonum aviculare.* Mature seed; aleurone layer present; endosperm filled with starch; embryo with well developed plumule at the side of the seed; nucellar tissue nearly obliterated; dotted line indicates plane of cross section shown in *fig.* 8; × 31.

FIG. 6. *Polygonum Convolvulus*, showing embryo in the octant stage and the endosperm in the free nuclear condition; × 64.

FIG. 7. *P. Convolvulus.* Mature seed; aleurone layer and starch filled cellular endosperm present; embryo at the side; nucellar tissue practically obliterated; dotted line indicates plane of cross section shown in *fig.* 10; × 20.

FIGS. 8–10. Fig. 8. *Polygonum aviculare;* fig. 9, *P. Persicaria;* fig. 10, *P. Convolvulus;* showing the relative position of the cotyledons in the three species; dotted lines indicate plane of longitudinal sections shown in *figs.* 4, 5, and 7; × 14.

FIG. 11. *Rumex crispus.* Mature seed; aleurone layer and starchy endosperm present; embryo at side of seed; nucellar tissue practically obliterated; dotted line indicates plane of cross section shown in *fig.* 13; × 31.

FIG. 12. *Rumex Acetosella.* Mature seed; starchy endosperm and aleurone layer present; embryo at side of seed; nucellus nearly obliterated; × 42.

FIG. 13. *Rumex crispus.* Cross section of mature seed showing position of cotyledons; dotted line indicates plane of longitudinal section shown in *fig.* 11; × 14.

FIG. 14. *Polygonella articulata*, showing the embryo in the octant stage supported by the characteristic long suspensor; endosperm in free nuclear condition; × 31.

FIG. 15. *P. articulata.* A little later stage in which the endosperm has become cellular except for the haustorium-like structure at the basal portion; embryo imbedded in the cellular endosperm; × 31.

FIGS. 16 AND 17. *P. articulata.* Successive stages in which the cotyledons have become well developed and the embryo sac practically filled with cellular endosperm; nucellar tissue reduced; × 31.

FIG. 18. *P. articulata.* Mature seed, showing cotyledons in section; aleurone layer, starchy endosperm, broken down nucellar tissue, and haustorium-like structure present; dotted line indicates plane of cross-section shown in *fig.* 19; × 31.

FIG. 18*a*. *Polygonella articulata,* showing detailed structure of micropylar portion of seed at stage shown in *fig.* 18; aleurone layer differentiated into a depleted and non-depleted region; starchy endosperm packed full of starch grains; × 163.

FIG. 19. *P. articulata,* showing position of cotyledons in the seed; dotted line indicates plane of longitudinal section shown in *fig.* 18; × 14.

FIG. 20. *Rheum Rhaponticum.* Mature seed; starchy endosperm and aleurone layer present; remains of nucellar tissue present at base of seed; dotted line indicates plane of cross section shown in *fig.* 21; × 14.

FIG. 21. *R. Rhaponticum,* showing position of the embryo in the seed; dotted line indicates plane of longitudinal section shown in *fig.* 20; × 14.

FIGS. 22–24. *Rumex crispus,* showing successive stages in the germination, in which the radicle of the young seedling appears through a rent in the micropylar portion of the seed and is clasped by the enlarged aleurone layer which appears outside the seed coat; × 20.

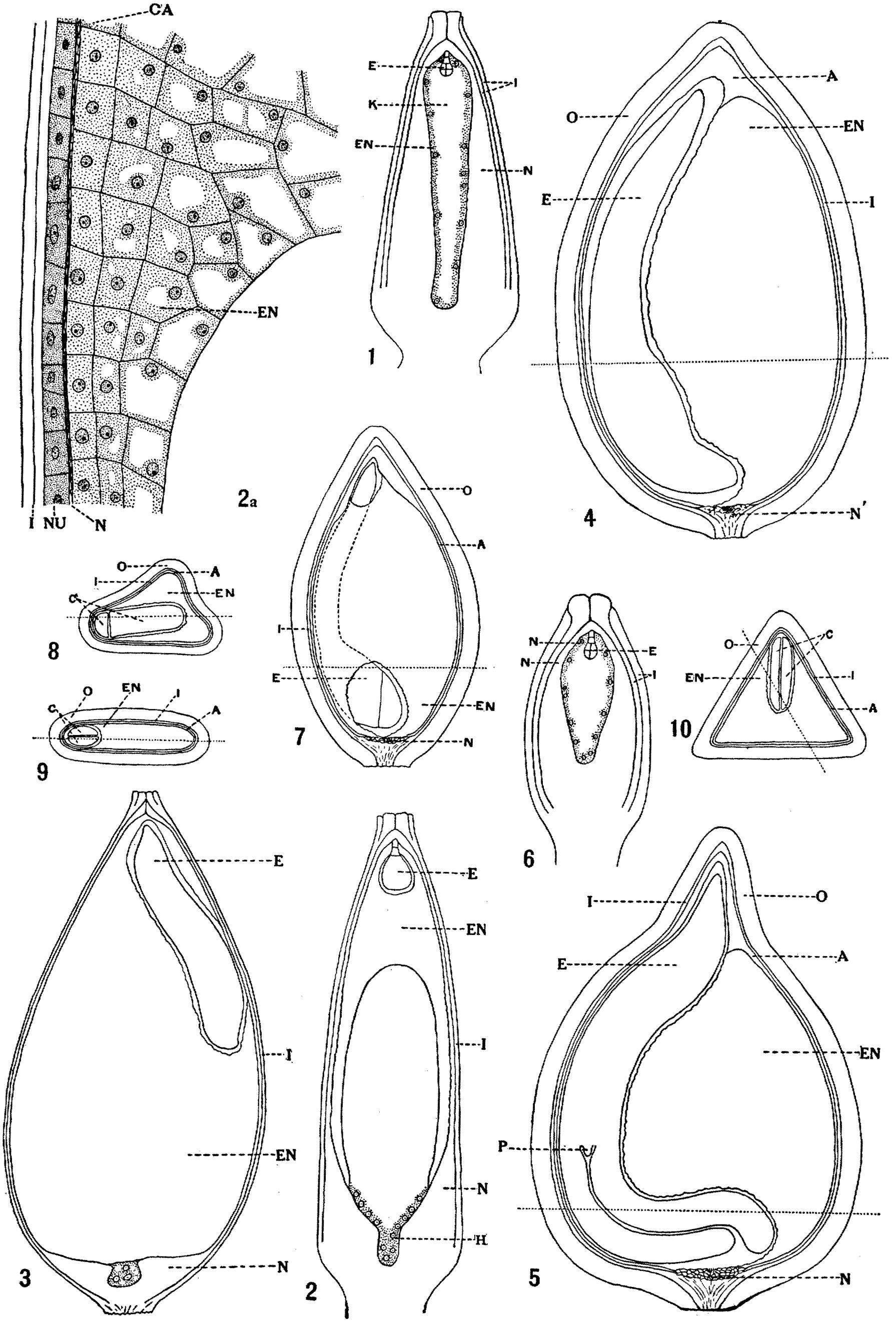
FIG. 25. *Fagopyrum esculentum,* showing an early stage in germination; × 14.

FIG. 26. *F. esculentum.* Cross section of seed at a stage somewhat later than that represented by the preceding figure; × 31.

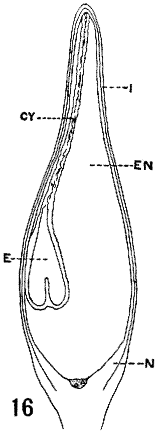
FIG. 27. *F. esculentum.* Late stage in germination; seed remains almost ready to drop off the cotyledons; × 14.

FIGS. 28 AND 29. *Polygonella articulata.* Successive stages in germination; enlarged micropylar portion of the aleurone layer appears outside of seed coat and clasps the young seedling; × 31.

FIGS. 30 AND 31. *Polygonum scandens.* Successive stages in germination similar to those of *Rumex crispus* shown in *figs.* 23 and 24; × 14.



WOODCOCK: SEED IN CERTAIN POLYGONACEAE.



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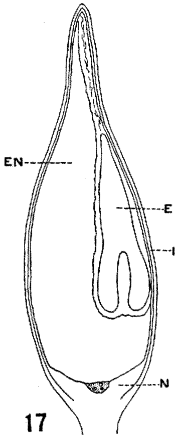

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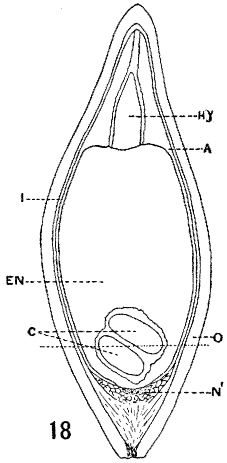

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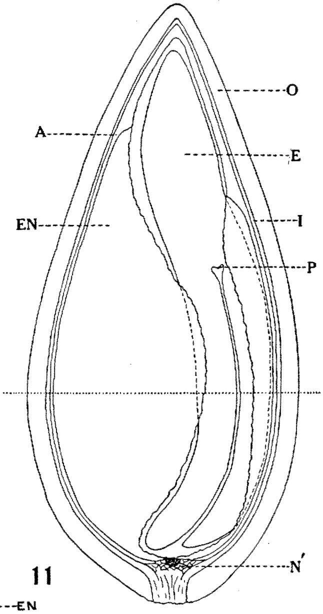

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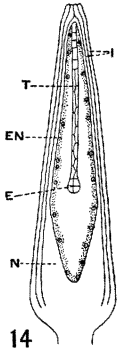

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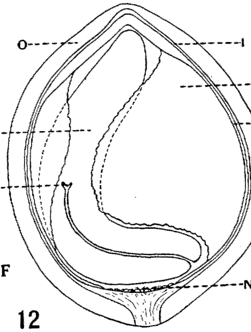

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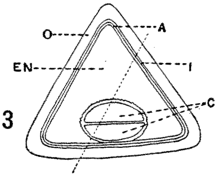

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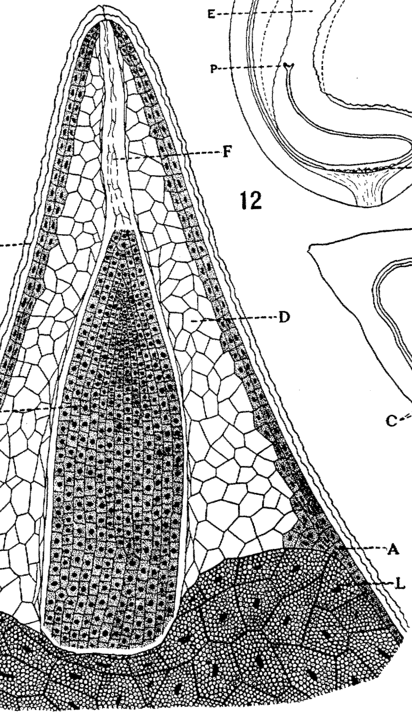

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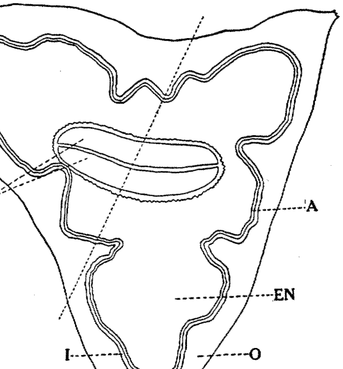

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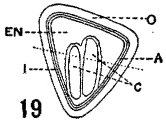

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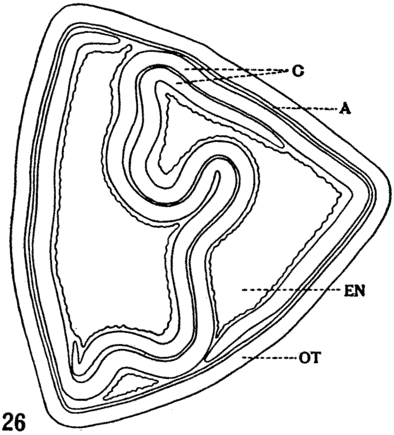
WOODCOCK: SEED IN CERTAIN POLYGONACEAE.



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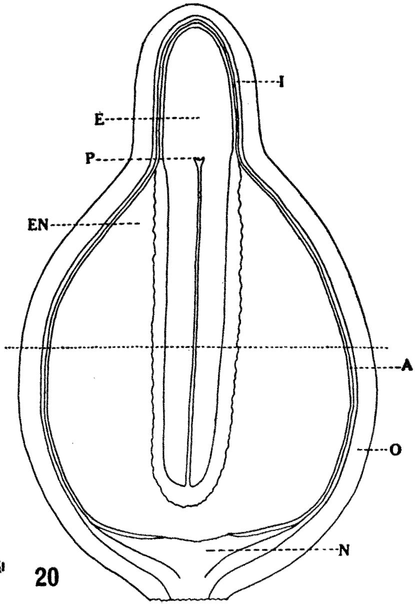

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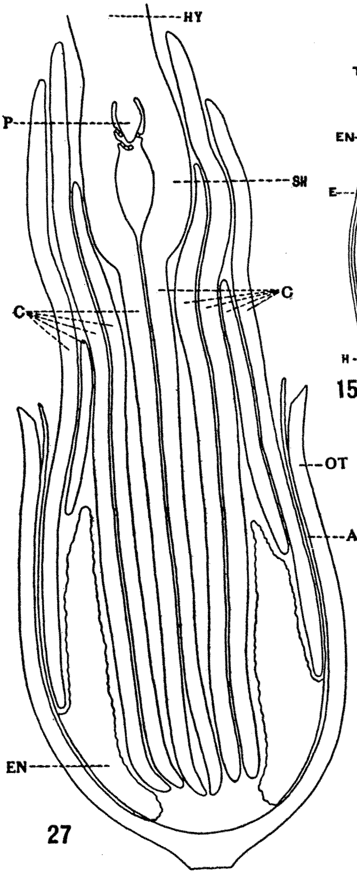

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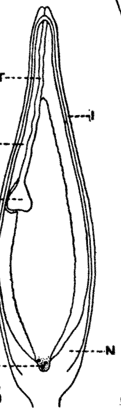

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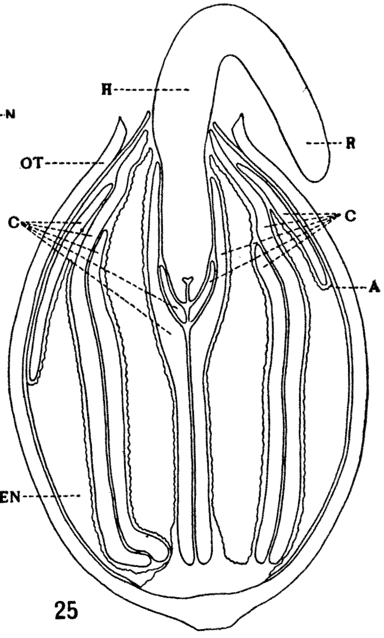

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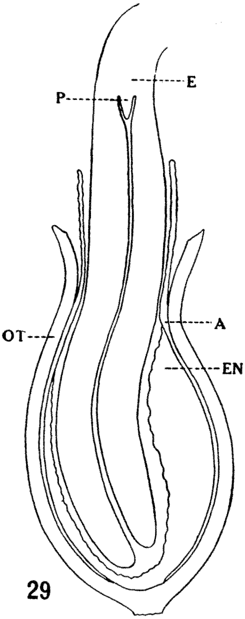
WOODCOCK: SEED IN CERTAIN POLYGONACEAE.



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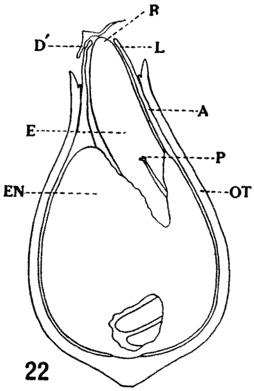

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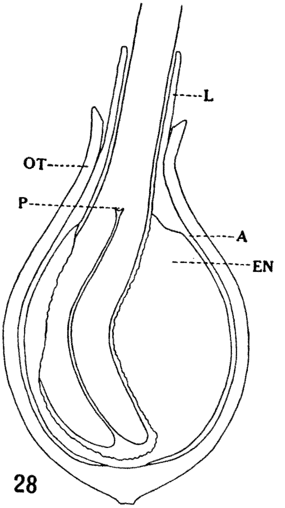

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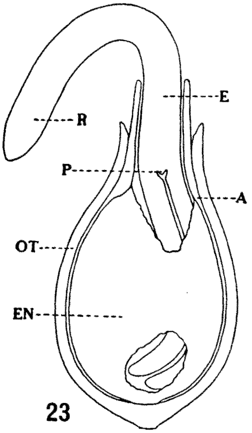
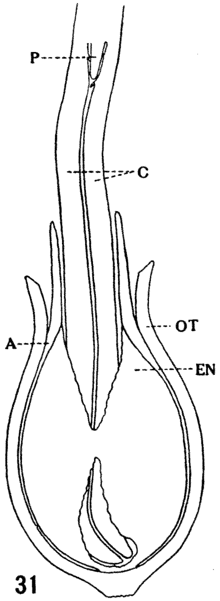
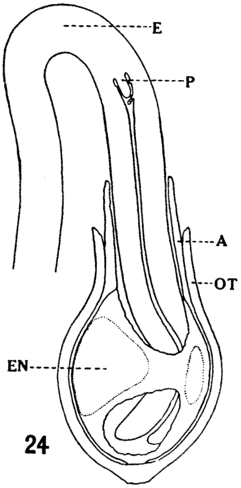


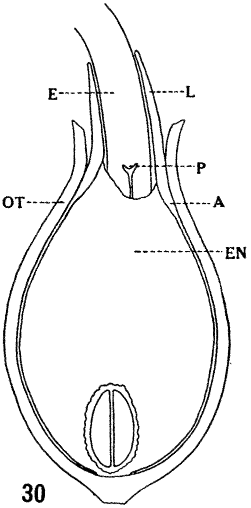
23



31



24



30

WOODCOCK: SEED IN CERTAIN POLYGONACEAE.